Pacific Science (1996), vol. 50, no. 1: 93–107

Reproductive Biology and Egg Abundance of the Yellowtail Scad or 'Ōmaka, *Atule mate* (Carangidae), in Kāne'ohe Bay, Hawai'i[1]

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ABSTRACT: Yellowtail scad or 'ōmaka, *Atule mate* (Cuvier & Valenciennes), spawn mostly between March and September or October, but there is considerable interannual variation in length of the season and egg density in Kāne'ohe Bay. Spawning occurs principally in open areas of the bay, with highest egg abundances in the southern section. Almost all adult 'ōmaka taken in the bay were reproductively active. More than two-thirds were males, which also routinely reached sizes larger than the largest female. Sex ratio and proportion of impending or recent spawners among females differed between day and night samples; all females in day samples were actively spawning. Adults probably move into the bay only for spawning and thus represent a biased sample of the sex ratio and spawning frequency of the population associated with the bay at any given time. Batch fecundity of females 188–232 mm standard length ranged from 63,000 to 161,000; mean relative fecundity was 741 eggs per gram. The standing stock of 'ōmaka associated with the bay during the peak spawning season is probably at least 800–1600 kg or 5000–10,000 adults. Current annual catch of 'ōmaka in the bay is a large fraction of the estimated standing stock, but the latter could be much higher if spawning frequency were underestimated or individual fish did not spawn throughout the entire season.

THE YELLOWTAIL SCAD, *Atule mate* (Cuvier & Valenciennes), is a small pelagic carangid that occurs in coastal waters throughout the tropical Indo-Pacific—from East Africa to Hawai'i. Although it nowhere contributes heavily to commercial fishing yields, it forms important fractions of the mixed catch of certain fisheries (Kuthalingam 1959, Oakley and Bakhsh 1989*a*) and is also sought by recreational and subsistence fishermen. In Hawai'i, where it is known as 'ōmaka, it is taken primarily in partially enclosed, often semiestuarine bays. In Kāne'ohe Bay, Hawai'i, 'ōmaka were formerly (before ca. 1970) sought by several small boats of handline fishermen every day during the summer months (pers. obs.), but both effort and catch have dropped since then. Several long-time fishermen whom I interviewed agreed that catch per effort also dropped dramatically during this period.

Little is known of many aspects of the 'ōmaka's biology. The eggs and larval development have been described (Kuthalingam 1959, Miller and Sumida 1974, Tsokur 1977) and growth investigated by Watarai (1973) and Oakley and Bakhsh (1989*b*). Distribution of eggs and larvae in Hawai'i has been reported by Watson and Leis (1974) and Miller et al. (1979). The former study showed that 'ōmaka spawn primarily between late spring and early fall, and both studies concluded that 'ōmaka rarely spawn outside of partially enclosed bays. Little else is known of its reproductive biology. In this paper I present data on 'ōmaka egg abundance, distribution, and seasonality as well as on size, sex, and reproductive condition of adults in Kāne'ohe Bay and attempt to estimate the size of the spawning stock in the bay relative to exploitation.

[1] This research was supported by the Hawai'i Division of Aquatic Resources, the University of Hawai'i Sea Grant College Program, and the University of Hawai'i, Hawai'i Institute of Marine Biology. This is UNIHI-SEAGRANT-JC-95-38 under NOAA Grant NA89AA-D-SG063. Manuscript accepted 2 March 1995.

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MATERIALS AND METHODS

'Ōmaka eggs in Kāne'ohe Bay were sampled by methods similar to those used for a 1984–1988 study of spawning by the Hawaiian anchovy, *Encrasicholina purpurea* (Clarke 1992). Vertical, surface-to-bottom plankton samples were taken with a 1-m-diameter net of 0.335-mm mesh. The net, with weighted bridle, was dropped open at the surface and allowed to fish to the bottom. It was then choked and retrieved by the choke line. For most stations sampled, water depth was 12–13 m, resulting in a total volume per sample of about 10 m^3. After retrieval, the catch was rinsed into the 0.335-mm cod-end, and the cod-end was removed, labeled, clipped shut, and placed in 4% formaldehyde-seawater.

Routine samples for 'ōmaka egg abundance were taken in the afternoon between 1300 and 1600 hours based on estimates of spawning time and incubation time from samples taken for studies of spawning timing of anchovies (Clarke 1989) and preliminary sampling throughout the daylight hours in March 1989. Newly spawned eggs first appeared in samples at 0800–0900 hours and were present until 1200–1300 hours. With few exceptions, eggs taken later were at least at the blastodisc stage. Late-stage eggs from the previous day's spawning were routinely found in morning samples, and a few were still present in early afternoon. These data agree with estimates of spawning time and incubation by Watson and Leis (1974) and Miller and Sumida (1974), respectively. The routine samples were thus taken after almost all spawning for the day had been completed and after most of eggs from the previous day had hatched.

Routine samples were taken at 14 stations in Kāne'ohe Bay that were selected based on occurrence of 'ōmaka eggs in samples taken throughout the bay during the 1984–1988 study of anchovy eggs (Clarke 1992). Five stations were along a roughly northwest/southeast transect of the northern and middle sections of the bay and nine others were in the southern basin (Figure 1). The number and general locations of the southern samples were selected to cover all parts of the basin where 'ōmaka eggs occurred and to intensively sample the area southeast of Coconut Island where egg abundance appeared to be routinely highest. Exact locations of all stations were dictated by prominent landmarks that could be used to locate the station in almost any weather.

All 14 stations were sampled weekly for most of the period between 20 June 1989 and 9 January 1992; nine stations (D, N, M, S, T, O, L, CC, and DC) were sampled every 2 weeks between 4 April and 13 June 1989. A single sample was taken at each of the five northern stations, and two replicate samples were taken at each of the nine southern stations. Other than the incomplete sampling between 4 April and 13 June 1989, one station was missed on each of 23 dates and two to three stations missed on five other dates. Mostly these were in the winter months when egg abundances were low and rough weather or early darkness prevented us from sampling one or two of the northern bay stations where egg abundance was rarely high. Stations with usually high egg abundances were missed on only six dates during the main spawning season. In addition, weather prevented sampling all of the northern bay stations on seven dates; egg abundances at other stations were high on only two of these dates.

In the laboratory, samples were concentrated and eggs of 'ōmaka counted for the entire sample under a dissecting microscope. New or recently spawned 'ōmaka eggs were counted separately from eggs from the previous day, which were readily distinguished by the advanced development of the embryo. Numbers of new 'ōmaka eggs per sample ranged from 0 to 500 routinely and were almost 1000 in several samples during the main season. 'Ōmaka eggs were readily distinguished from other fish eggs present [over 90% of which were those of the engraulid *Encrasicholina purpurea* or the carangid *Gnathanodon speciosus* (Forsskål)] by criteria given in Watson and Leis (1974). It is possible that eggs of other carangids or certain other percoids with pelagic eggs that are similar to those of 'ōmaka could have been present and counted as 'ōmaka eggs, but such errors were probably minor and sporadic at the worst.

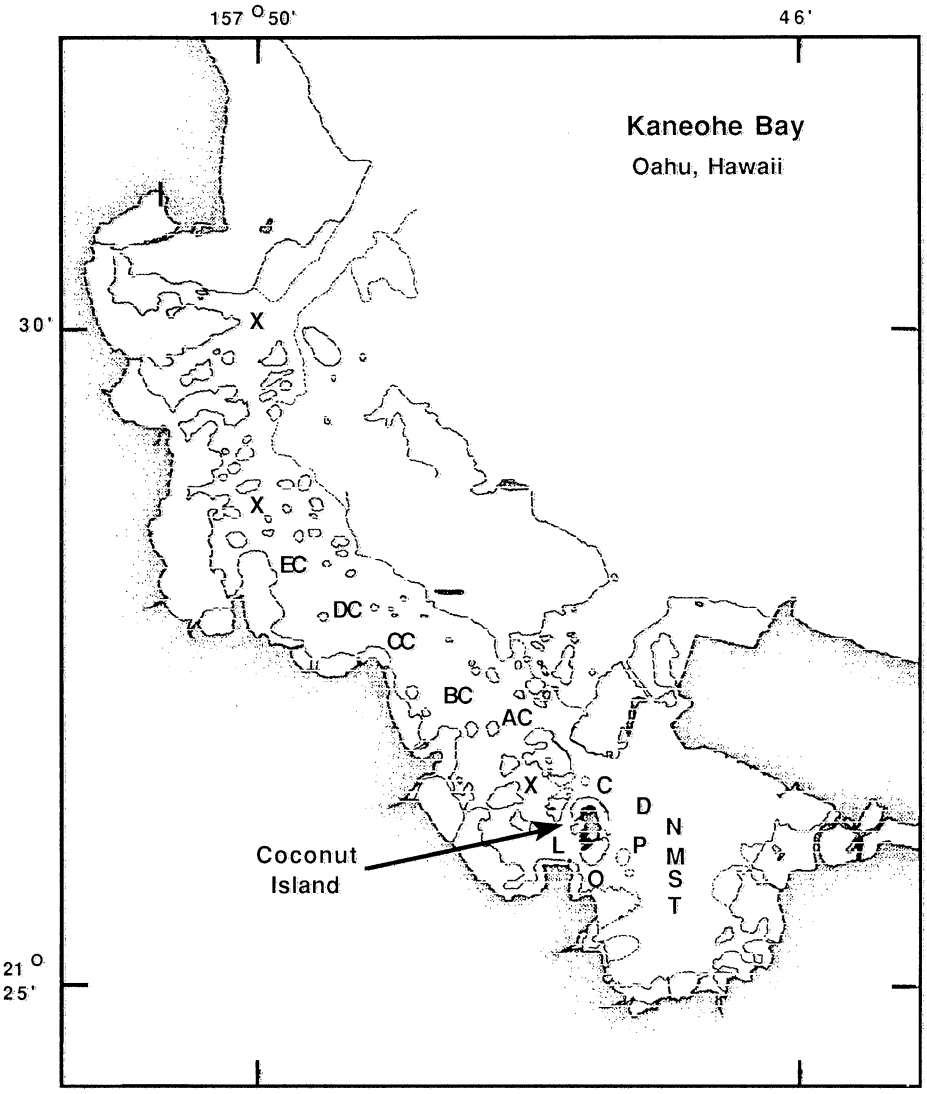

FIGURE 1. Map of Kāne'ohe Bay, Hawai'i, showing locations of gill net and egg sampling stations for investigation of *Atule mate* during 1989–1991. Gill net stations were at three locations marked "X" plus egg stations CC, AC, D, and S.

Watson and Leis (1974) indicated that other eggs that could be confused with those of 'ōmaka during routine counting were extremely rare within the bay. Their data on larvae as well my own examinations of several hundred plankton tows indicated that larvae of most percoids with pelagic eggs, including other carangids, are absent or extremely rare in the bay and only occur sporadically in the channel connecting the bay with coastal waters. For example, a series of nighttime oblique tows with paired 70-cm-diameter nets taken throughout the bay for other purposes in April, June, and September of 1991 caught 750 larvae of 'ōmaka and *G. speciosus* and none of other carangids or of

other percoids with pelagic eggs (unpubl. data).

Preliminary surveys, some conducted during the previous study of anchovy eggs (Clarke 1992), indicated that newly spawned ʻōmaka eggs very rarely were found over areas where bottom depth was <10 m; consequently, the area represented by each station was delimited by the locus of points equidistant from that station and adjacent stations or by the 9.15-m (30-ft) contour drawn from a hydrographic chart of the bay. The boundaries for the northernmost (EC) and southernmost (T) stations were based on either the 9.15-m contour or preliminary surveys. The areas represented by each of the stations were unequal. For the nine southern stations, mostly separated by about 0.5 km, areas ranged from 0.13 to 0.46 km^2, and the total area was 2.67 km^2. The areas for the five more widely spaced (about 1 km) northern stations ranged from 0.70 to 1.37 km^2, and the total area was 4.65 km^2 or 63.5% of the combined northern and southern stations.

To estimate total egg abundance for a given date, the eggs per sample data were converted to eggs per m^2 using the mouth area of the net (0.785 m^2) and multiplied by the area represented by the station. Data for the individual stations were then summed and corrected for any missing stations using the average percentage contributions of the missed stations on other dates. Most dates when stations were missed either were during the winter when egg abundance was very low or amounted to $\leq 6\%$ of the total. This was not the case for the five dates sampled in early 1989 (see above), and results for these must be considered less reliable. Corrections for two dates when the northern stations were missed during the main spawning season were about 40% of the adjusted total estimate, and corrections for six other dates during the main season when stations of usually high abundance were missed were 8.5–12.1%. None of these latter eight corrections resulted in any abrupt changes in trend of the data.

Data from station C on 19 August 1991 were also adjusted because of an inordinately high number of eggs (5209) in one sample. This catch was over five times the highest values recorded at any of the stations with usually high abundance and almost 20 times the next highest catch at station C; inclusion of this catch would have resulted in a total egg abundance estimate almost three times higher than that on any other date. All the ʻōmaka eggs in this sample were in the very early blastodisc stage as opposed to a mixture of early stages typical of other samples. Thus this sample probably resulted from a chance encounter with a patch of very recently spawned eggs and means that some ʻōmaka spawn after the time when the routine sampling began. That such a catch was encountered only once during the entire survey indicates that such events are infrequent and probably do not materially affect the overall picture of egg abundance.

The error associated with estimated egg abundances is uncertain, and to specify it rigorously would have required routinely taking a large number of replicate samples at each station. Preliminary sampling with four to six replicates per station and examination of agreement between replicates at the southern stations indicated that variability was a function of egg density, location, and also date—the latter probably due to different degrees of tidal or wind mixing. In general, however, replicate samples were within 5% of each other in most cases where eggs per sample were >100. Nevertheless, some of the short-term variability in egg abundance estimates was probably due to sampling error—especially for the more widely spaced northern stations where only a single sample was taken on each date. Consequently, the estimates were smoothed using a three-point moving average, and the estimates based on the southern stations are given separately from the total for the entire bay.

I also used estimates of ʻōmaka egg abundance derived from an unpublished research report based on samples taken 20 yr previously, in October–December 1969. (I was unable to obtain any other earlier data on ʻōmaka egg abundance based on samples that covered the entire water column.) ʻŌmaka eggs had been counted from vertical plankton samples taken on seven dates at eight

stations in Kāne'ohe Bay (locations: about 1 km south of station T, between stations N and M, about 1 km east of station N, and near stations L, C, AC, CC, and EC). The data had been pooled for the two stations near station N and for the two near CC and EC and had been presented as estimates of total eggs for six different sections of the bay, but sufficient details were given to convert results presented into six estimates of egg density for each of the seven dates.

Adult 'ōmaka were taken with gill nets set in the deep (10–13 m) areas of the bay. Preliminary testing indicated that a mesh size of 6.35 cm (2.5 in.) was the most effective. Multifilament nets were used for overnight sets (roughly 1600–0800 hours). Standard sets with nets 40 m long and 4 m high were made at roughly quarterly intervals from June/July 1990 through June/July 1991 near egg stations CC, AC, D, and S; at a station between the patch reefs that separate the northern and southern sections of the bay; and at two stations at the northern end of the bay (Figure 1). Other overnight sets with slightly different-sized nets were made during the spawning season near egg stations D and S. 'Ōmaka were also recorded from over 50 overnight gill net sets made for other purposes during the same period at various other sites and situations throughout the bay. Monofilament nets, 40 m long and 6 m high, were used to collect 'ōmaka during the daylight hours; these were set at 1000–1500 hours for a few hours near stations O, P, or S. 'Ōmaka caught were taken to the laboratory immediately after nets were retrieved, where standard length was measured to the nearest 1 mm, gonads were removed and preserved in 4% formaldehyde-seawater, and somatic or gonad-free weight was determined to the nearest 1 g.

Preserved gonads subsequently were weighed to the nearest 0.1 g and gonad to somatic weight ratios (G/S) were determined. For all females, a small sample of the ovaries was placed on a slide, teased apart, and examined under a compound microscope. Development and opacity of the largest oocytes were recorded, and diameters of about 100 oocytes >0.10 mm were measured to the nearest 0.01 mm using an ocular micrometer. Because only a minority of the females had distinct, separated size-frequency modal groups of advanced oocytes, the diameter of the largest unhydrated oocyte (LMX) was used as an indicator of overall oocyte size and development. In many cases where a partially separated advanced modal group was discernible from size-frequency data, the oocytes associated with that group could be distinguished from other oocytes by their greater opacity. Presence of hydrated, but unovulated eggs in the tissue was noted, as was presence of ovulated eggs in the lumen or oviducts.

Batch fecundity was estimated for females with a distinct, separated size-frequency modal group of advanced oocytes or with a partially separated advanced group that could be clearly discriminated by greater opacity. A sample of about 1% of the weight of one ovary was placed on a clean glass slide and all the oocytes in the advanced group were counted. The material on the slide was then rinsed into a preweighed aluminum pan with distilled water, and the remaining part of the ovary placed in another pan. The sample and ovary were dried for 24 h at 60°C, the pans were reweighed after cooling under vacuum in a desiccator, and the dry weights were determined by subtraction of the pan weights. The dry weight of both ovaries was calculated from the determined dry weight of the ovary sampled plus the wet weight of the other ovary multiplied by the dry/wet weight ratio for the ovary sampled and dried. Total batch fecundity was then calculated from the number of eggs or oocytes in the sample, the dry weight of the sample, and estimated dry weight of both ovaries. Relative batch fecundity was calculated as batch fecundity divided by the somatic weight of the female.

For 46 females without ovulated eggs, one of the ovaries was sectioned, stained with hematoxylin/eosin, and mounted on a slide. The sections were examined for presence of postovulatory follicles (POF), an indication of recent spawning, and for oocytes with migratory nuclei or coalescing oil droplets, indicators of impending spawning. The slides, identified only by code numbers, were exam-

ined independently by two observers. All POF recorded were readily evident, and there were no disagreements between observers as to the presence or absence of POF.

Dry weight per spawned egg was estimated from samples of 10 preserved eggs each taken from females with ovulated eggs in the oviducts. The samples were rinsed in distilled water, placed in preweighed pans, dried for 2–3 hr at 60°C, reweighed, and the estimated weight per egg calculated.

RESULTS

The egg abundance data indicated that the main spawning season for 'ōmaka is from about March to September–October, but some eggs are present into December (Figure 2). 'Ōmaka eggs were absent from the samples for only one extended period during January–February 1990; low numbers were present during the same period in 1991. Total egg abundances were $1–2 \times 10^8$ during the peaks of the spawning seasons of 1989 and 1990, but values were roughly twice as high for most of the season in 1991. The 1991 season also was longer in that relatively high abundances occurred during much of October through December.

For most sample dates and overall, the southern basin of the bay accounted for the majority of eggs. There were no extended periods when most spawning was in the northern section. For 73 dates when all stations were sampled and total egg abundance

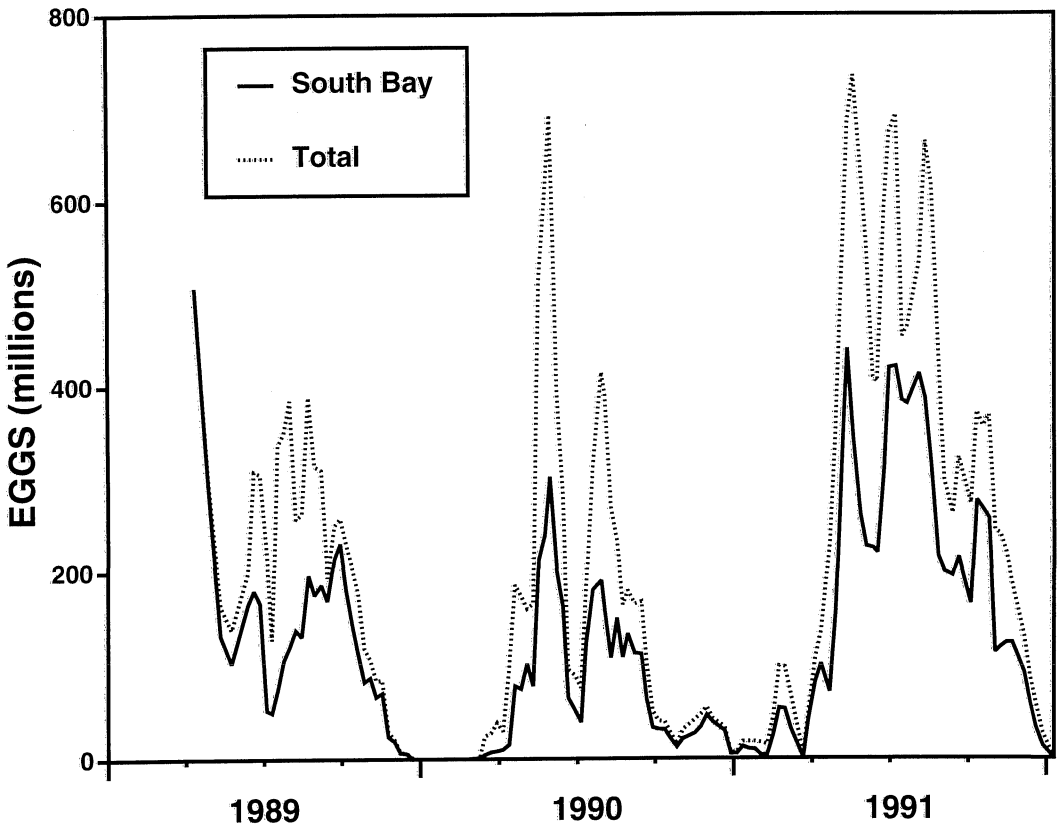

FIGURE 2. Estimated abundance (in millions) of eggs of *Atule mate* in Kāne'ohe Bay during 1989–1991. Lines connect three-point moving averages of the raw estimates. Solid line indicates estimates for the southern section of the bay alone; dashed line indicates totals for the entire bay.

was at least 25×10^6, the southern stations, which represented only 36.5% of the total area, accounted for a mean of 62.2% of the estimated eggs. The highest mean contribution among stations was, however, for station CC in the northern section. It contributed 16% to total estimated egg abundance on the average and over 50% on several different dates. Another northern station, DC, and four southern stations, N, M, S, and P, each contributed 9–12% on the average (Table 1). Each of these as well as stations D and T contributed over 40% to the total on one or more different dates. All stations with high contributions were in open areas of the bay with few patch reefs. The peripheral southern stations (C, O, L) and the stations in the narrower parts of the north section (EC, BC, AC) contributed little on the average and rarely as much as 10–20% to the total (Table 1). (Note that one extremely high catch of eggs from station C was not included in the analyses [see *Materials and Methods*].)

TABLE 1

PERCENTAGES OF TOTAL AREA (7.3121 km^2) REPRESENTED, MEAN AND MAXIMUM PERCENTAGES OF TOTAL *Atule mate* EGGS PRESENT, AND MEAN AND MAXIMUM DENSITIES OF EGGS FOR 14 STATIONS IN KĀNE'OHE BAY, HAWAI'I

STATION	% AREA	MEAN % EGGS (MAX.)	MEAN EGGS/m^2 (MAX.)
EC	9.7	2.8 (17.5)	9.924 (191)
DC	18.7	9.6 (58.3)	24.349 (290)
CC	13.3	15.9 (76.8)	60.261 (531)
BC	12.2	6.9 (44.1)	21.907 (201)
AC	9.6	2.5 (21.2)	7.709 (109)
C	5.0	3.2 (27.2)	18.507 (363)
D	4.6	7.6 (61.3)	50.223 (786)
N	6.2	10.0 (44.9)	57.357 (554)
M	3.6	12.1 (45.9)	130.856 (826)
S	3.8	11.9 (51.7)	124.315 (699)
T	4.8	6.6 (74.5)	68.511 (1,452)
P	3.8	9.3 (50.4)	85.403 (873)
O	2.8	1.1 (20.5)	9.924 (176)
L	1.7	0.4 (5.1)	4.256 (39)

NOTE: Stations are listed in roughly north to south order (see Figure 1). Values for eggs are based on data from 73 dates between June 1989 and January 1992 when all stations were sampled and total egg abundance was $\geq 25 \times 10^6$. Minimum percentages and densities were zero for all stations except M, where the minimums were 0.1% and 1.91 eggs per m^2, respectively.

The relative contributions by individual stations to total egg abundance were partly a function of areas represented, but egg densities were much higher at the more closely spaced southern stations. Mean egg densities (Table 1) at stations M and S were over twice those at station CC, the most important in terms of average contribution to the total, and means at stations D, N, T, and P were comparable with or greater than that at CC. Both mean and maximum egg densities of stations that contributed little to total abundance were, however, low regardless of the area represented.

The data from 1969 indicated that 'ōmaka egg densities and distribution were generally similar to those presented here. For the two stations most representative of the southern section of the bay, densities for the seven dates averaged 92 eggs per m^2 with a range of 45–264, well within that observed, for example, at stations N and M in the study reported here. Egg density for the two stations close to CC and EC was zero for six of the dates and 410 eggs per m^2 for one; this agrees with the results of the study reported here, which show that egg density at station CC occasionally exceeded that of stations in the southern section of the bay. Egg densities at the other stations averaged only 12.32 eggs per m^2 (range, 0–55) and indicated that, as in the study reported here, egg densities were usually low or negligible in the areas near stations L, C, and AC and south of the area represented by station T. That densities on the order of those observed in the 1969 study occurred late in the year indicates that 1969 may have been like 1991 in that heavy spawning continued past September.

A total of 370 adult 'ōmaka was taken, 250 from overnight sets and 120 from daytime sets. 'Ōmaka in the overnight sets appeared to have been caught mostly in the morning just before the net was retrieved. The majority were still alive, and few were damaged or putrid, as would be expected had they been in the net for more than a few hours. Standard length (SL) ranged from 163 to 254 mm (mean = 211.9 mm) and somatic weight from 68.1 to 306.6 g (mean = 175.1 g). The overall ratio of males to females was

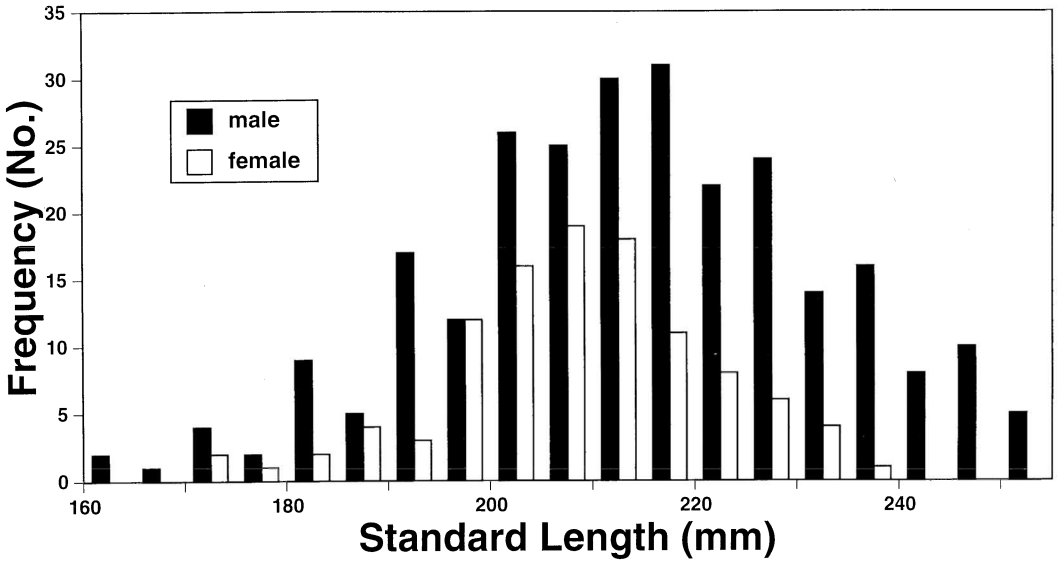

FIGURE 3. Size frequency of 263 male (solid bars) and 107 female (open bars) *Atule mate* taken in Kāne'ohe Bay during 1989–1991. Individuals originally were measured to the nearest mm, but data have been grouped by 5-mm increments for clarity in presentation.

2.46; the ratio was 2.73 for the overnight sets and 2.00 for the daytime sets. The lower value for daytime catches was mostly due to a single catch of 78 'ōmaka with a sex ratio of 1.89; the ratio for the remaining day catches was 2.23, still somewhat lower than that for the night catches. Mean size of males was slightly larger than that of females (213.6 mm SL and 183.2 g versus 207.7 mm and 155.3 g). The size compositions differed between the sexes (Kolmogorov-Smirnov test, $P < 0.01$) and indicated that the uneven sex ratio was in part due to the absence of females over 237 mm (Figure 3); nevertheless, the ratio for fish smaller than the largest female was still 2.20 ($n = 317$) in favor of males.

Between June 1990 and April 1991, catches of 'ōmaka per set for standard overnight sets ranged from zero to eight; the means were about two per set for both northern and southern sections of the bay and all seasons. In June–July 1991, there were two high catches, 27 and 13 per set, and the mean catch per set at the remaining five stations was 6.2, much higher than in the same months of 1990. Catches from other overnight sets, all in the southern section, ranged from 0 to 10 per set. Two of the daytime sets near station S caught 78 and 19 'ōmaka; catches of other daytime sets ranged between one and five. All but 12 of the total 'ōmaka taken were from sets in 10–13 m depth in the open areas of the bay. The others were all from overnight sets perpendicular to reef edges and were usually found at the deep-water end of the net. No 'ōmaka were taken in numerous sets in shallow nearshore areas, reef tops, or parallel to reefs.

For both sexes, all sizes of 'ōmaka taken appeared to be in spawning condition during March–December. (Unfortunately, there were no fish from January or February, when 'ōmaka eggs were absent or uncommon.) Vitellogenic oocytes ≥ 0.35 mm were present in all but three females, and G/S was >0.02 for the great majority except during March and December (Figure 4). Most G/S values >0.06 were for individuals carrying hydrated ova. The smallest female taken (171 mm SL) had a low G/S (Figure 5), but carried vitellogenic oocytes. Male G/S was >0.01 for all but a few individuals taken in March

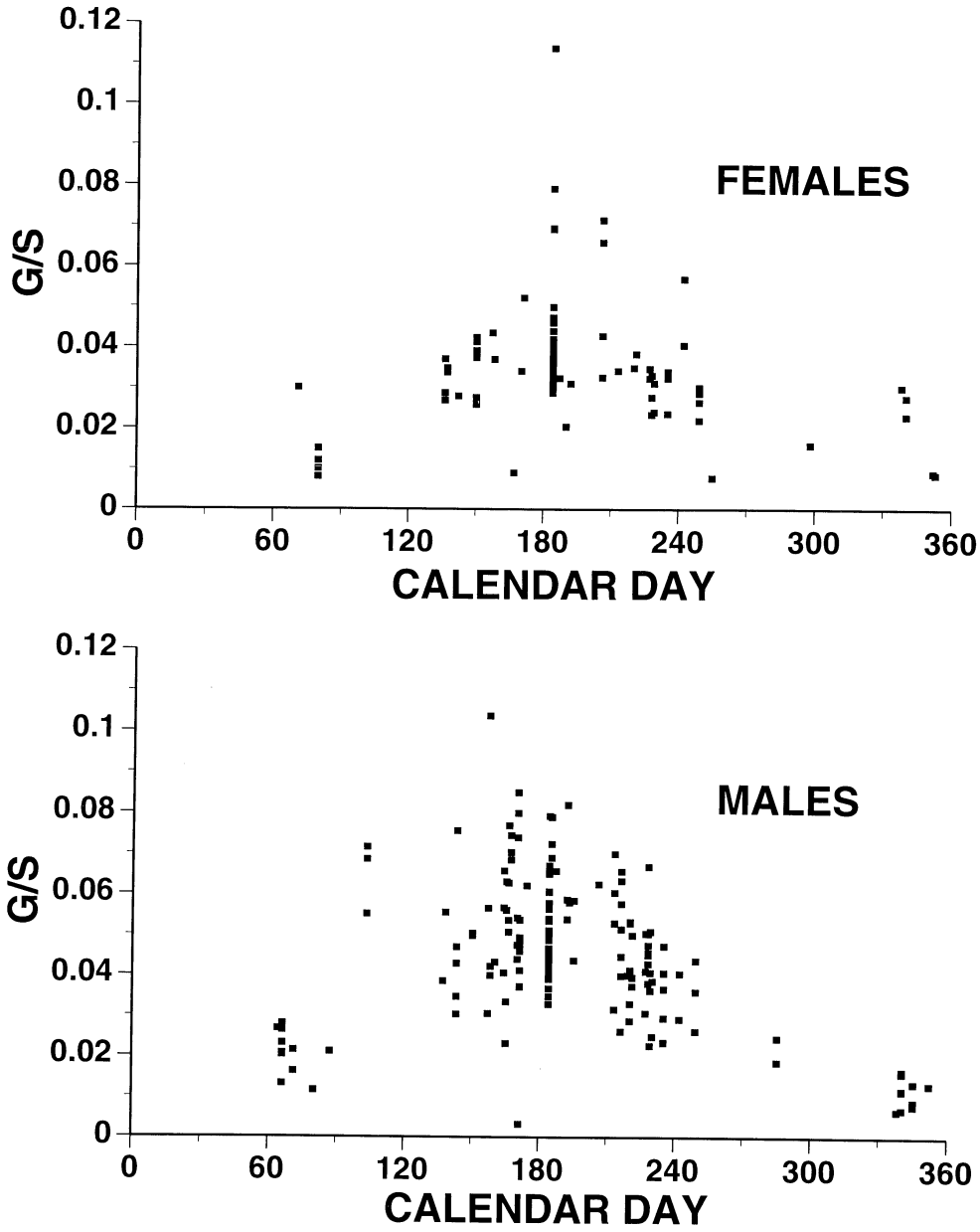

FIGURE 4. Plots of gonad to somatic weight ratios (G/S) versus calendar day for 83 female and 163 male *Atule mate* taken in Kāne'ohe Bay during 1989–1991.

or December and for a single inactive male taken in June (Figure 4). The smallest male taken was clearly mature (Figure 5). In contrast to most fishes, G/S of males was routinely as high as that of females.

Oocyte development and size-frequency distributions of 'ōmaka were very similar to those of the carangid *Selar crumenophthalmus* (Bloch) (Clarke and Privitera 1995). Microscopic examination of ovarian tissue from 75

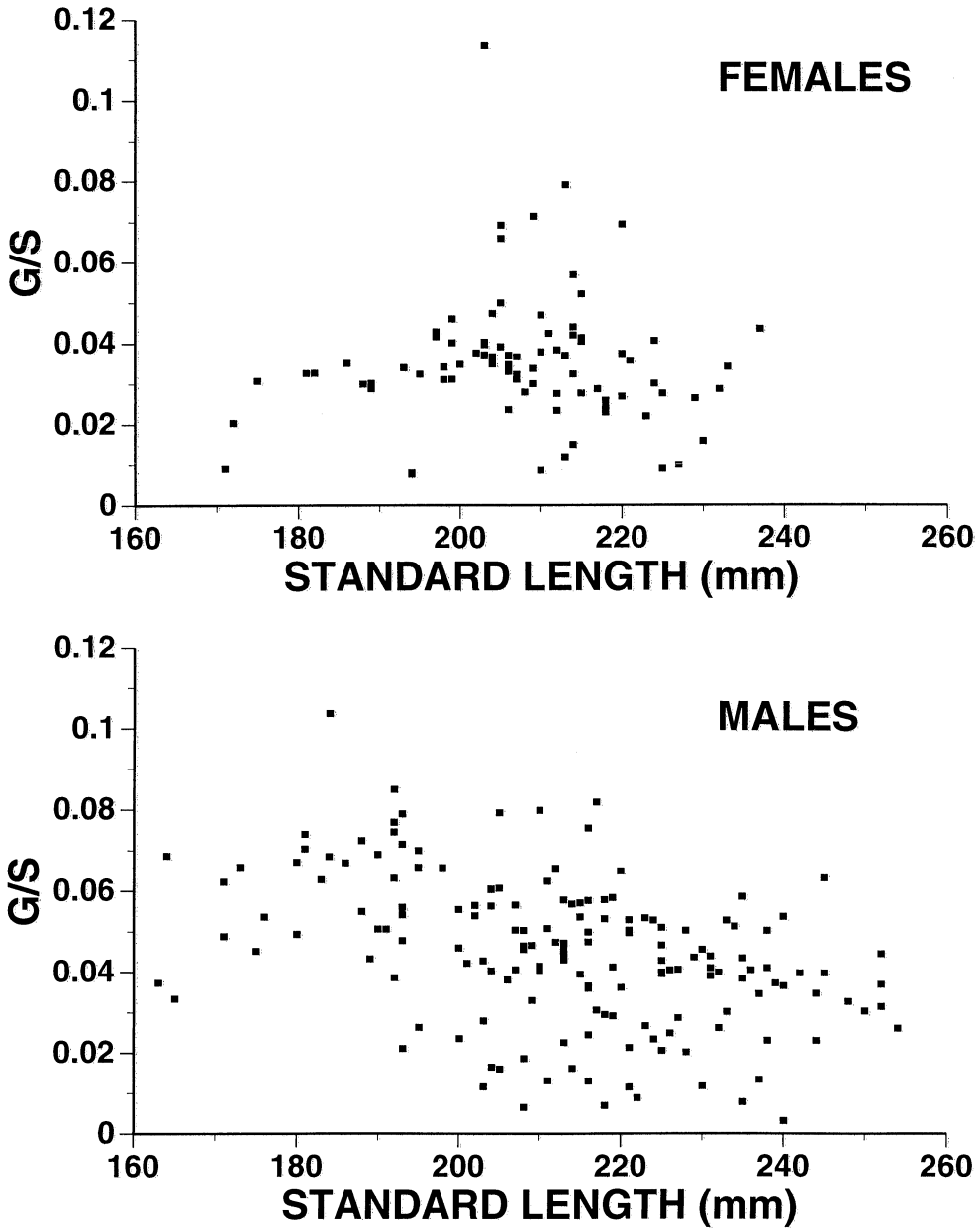

FIGURE 5. Plots of gonad to somatic weight ratios (G/S) versus standard length for 83 female and 163 male *Atule mate* taken in Kāne'ohe Bay during 1989–1991.

mature females indicated that vitellogenesis begins at an oocyte diameter of about 0.25 mm. By 0.30–0.35 mm, the oocytes are densely opaque with yolk. Maximum LMX was 0.54 mm, but few females with LMX >0.50 mm were taken. In 13 individuals, there were a few oocytes 0.03–0.10 mm larger than the largest associated with the advanced modal group. A size-frequency modal group of advanced oocytes was present in about

half the ovaries examined, but was rarely distinctly separated by size from smaller oocytes. The oocytes in the left-hand "tail" of the advanced modal group could, however, usually be discriminated from less-developed, but similar-sized oocytes by differences in opacity. Of the 46 ovaries prepared for histological examination, only one (LMX = 0.54 mm) had oocytes in the migratory nucleus stage, and only one other (LMX = 0.52 mm) was in the early stages of coalescence of the oil droplet.

Hydration apparently begins at about 0.50–0.55 mm; spawned eggs are about 0.70 mm in diameter. Hydrated ova were found in 26 females; in most cases these were ovulated and free in the lumen and oviducts, indicating the females were either spawning or just about to spawn. Four females (two night, two day) carried only a few unovulated hydrated ova and no ovulated ova. Subsequent histological examination (see below) showed that postovulatory follicles were present in all four; thus, the hydrated ova were apparently left over from recent spawning. Dry weights of five samples of 10 ovulated eggs each from two different females ranged from 0.130 to 0.137 mg; the mean value indicated that individual egg weight was 0.0134 mg.

Histological preparations were made for ovaries of 46 of the 75 mature females for which oocyte size-frequency data were available, and large numbers of ovulated eggs were present in 21 others (Table 2). POFs were present in 18 of 23 females from overnight sets; LMX of these was 0.35–0.46 mm. POFs of tropical fishes are typically unrecognizable after $\leq$ 24 hr (Hunter et al. 1986, Clarke 1987, Davis and West 1993). Thus these ʻōmaka had probably spawned the previous day. Among the fish from overnight sets that were not examined histologically, there were six without hydrated oocytes and LMX = 0.38–0.44 mm; these too most likely had spawned the previous day. One of the night fish without POF and LMX = 0.42 mm carried a large number of hydrated, but unovulated ova. Two others had large oocytes (LMX = 0.52–0.54 mm) that in one case were at the migratory nucleus stage and in the other with the oil droplets beginning to coalesce. These plus 12 other night fish with ovulated

TABLE 2

SUMMARY OF DATA FROM OVARIES OF 75 MATURE FEMALE *Atule mate* TAKEN IN OVERNIGHT AND DAYTIME GILL NET COLLECTIONS IN KĀNEʻOHE BAY, HAWAIʻI

COLLECTION	POF[a]	STAGE[b]	NO.[c]	LMX[d] (mm)	SPAWNING DAY[e]
Overnight sets					
	+	Oo	16	0.35–0.46	Previous
	+	H (few)	2	0.41–0.42	Previous
	×	Oo	6	0.38–0.44	? previous
	×	Ov	12	0.39–0.43 + 0.49	Next
	0	H, pre-H	3	0.42–0.52	Next
	0	Oo	1	0.49	? next
	0	Oo	1	0.45	Neither
	×	Oo	1	0.47	?? neither
Day sets					
	+	Oo	21	0.38–0.46	Same
	+	H (few)	2	0.46–0.47	Same
	×	Ov	9	0.42–0.54	Same
	×	Oo	1	0.41	? same

[a] +, presence of postovulatory follicles; 0, absence of postovulatory follicles; ×, not examined histologically.
[b] Most advanced oocytes or eggs: Oo, unhydrated oocytes; H, hydrated but unovulated eggs; Ov, ovulated eggs; pre-H, large unhydrated oocytes at the migratory nucleus or coalescing oil droplet stage.
[c] Number of females in each category.
[d] Sizes of the largest unhydrated oocytes.
[e] Probable day of most recent or impending spawning relative to the time of capture.

ova were almost certainly going to spawn the next day. LMX was 0.49 in one of the remaining night females without POF; she was also likely to have spawned the next day. The remaining female without POF (LMX = 0.45) apparently neither had spawned the day before nor was ready to spawn the next day. Based on LMX (0.47 mm), the one remaining unexamined female was probably the same, but could have been ready to spawn the next day. Thus at least 18 and probably 24 of the 42 females from overnight sets had spawned the previous day and at least 15 and possibly 16 were going to spawn the next morning (Table 2).

All of the day-caught females either appeared to have just spawned or were in the process when caught. All 23 examined histologically had POF, and nine of the unexamined fish carried ovulated eggs. LMX of the remaining unexamined fish was 0.41 mm and within the range of those with POF (Table 2).

Batch fecundity was estimated for 20 females 188–232 mm SL with LMX of 0.38–0.49 mm. In 10 of these, the advanced modal group of oocytes was separated in size from smaller, less-developed oocytes. In the remaining 10, the small ooctyes in the advanced group overlapped less-developed oocytes, but could be discriminated by their greater opacity. There was no apparent difference between the two groups in fecundity or relative fecundity. Fecundity ranged from 63,000 to 161,000 and was poorly related to somatic weight (r^2 = 0.16 for the logarithms of weight and fecundity and 0.14 for the untransformed data). Mean relative fecundity was 741 eggs per gram (range, 420–1125). Estimated batch fecundity for a female of average weight (155 g) is about 115,000 eggs. Based on the estimated dry weight per egg and assuming that dry/wet weight ratio of ʻōmaka is 25–30%, the cost (in terms of dry weight) of an average batch of eggs is 3.3–4.0% of body weight.

DISCUSSION

The spring to fall spawning season observed for ʻōmaka in Kāneʻohe Bay agrees generally with earlier estimates by Watarai (1973) and Watson and Leis (1974), but the data for 1991 show that occasionally heavy spawning can continue well into the winter. Not only was the spawning season longer in 1991, but egg densities were also higher than in 1989 and 1990. The gill net catch rates in the summer of 1991 were also higher; thus the higher egg densities were probably a result of greater numbers of adults present in 1991 rather than of increased fecundity or spawning frequency. There are no obvious factors correlated with these variations. Because, as suggested below, adult ʻōmaka probably occur outside enclosed areas when they are not actively spawning, the factors influencing the numbers moving into the bay in any given year may operate in coastal waters and be unrelated to conditions in the bay itself.

Size at maturity is not directly evident from these results, but other data indicate that it is probably about 160 mm, or near the size of the smallest fish taken in this study. Watarai (1973) stated, apparently based on development of captive fish, that ʻōmaka mature at about 150 mm. In Kāneʻohe Bay, juvenile ʻōmaka up to about 75 mm regularly are seen and taken near jellyfish and floating objects during the summer, but neither these collections nor my records of over 50 ʻōmaka taken in the bay by gill net, handline, or purse seine over the previous 20 yr included fish between 100 and 160 mm. (The gill nets used in this study and earlier would have retained ʻōmaka considerably <160 mm had they been present.) The only ʻōmaka in this size range I have ever seen were about 100 specimens 100–145 mm SL that I measured from a collection in an enclosed pond in April 1968. These had apparently entered the pond as small juveniles through mesh barriers and had been trapped there with growth. Otherwise it appears that after juveniles reach a length of 75–100 mm they leave the bay and do not return until sexually mature, and thus that the smallest adults caught in the bay are probably close to the minimum size at maturity. Oakley and Bakhsh (1989*a*) reported differential movement related to maturity in the Red Sea; preadult-sized fish (135–

160 mm) were present in the coastal fishery catches only during the second half of the year.

Reproductive data for 'ōmaka are very similar to those reported for a slightly larger pelagic carangid, *Selar crumenophthalmus* (Clarke and Privitera 1995). Both species spawn during the day over similar seasons. Egg weight is similar in the two species, but relative fecundity and the estimated cost per batch of 'ōmaka are somewhat higher than those of *S. crumenophthalmus*. In both species, as well as in *Decapturus macarellus* (Cuvier) (Clarke and Privitera 1995), advanced modal groups of oocytes are often not completely separated by size from less-developed oocytes, and there is evidence that, even after hydration, a small fraction of the advanced modal group is not always ovulated and spawned with the batch.

The routine capture of male 'ōmaka considerably larger than the largest female is anomalous for most small pelagic fishes, and there are no reports of comparable sexual size differences for other carangids. The observed differences in maximum size for 'ōmaka could be an artifact caused by differential distribution and movement, but it is difficult to postulate why large females but not large males would avoid the bay. The results thus indicate that male 'ōmaka have higher growth rates or lower mortality rates than females. Regardless of the cause, the number of males larger than the largest female was by itself insufficient to account for the preponderance of males among the samples from the bay.

Apparent sex ratio varies with location and time in other carangids (Naughton et al. 1986, Tiews et al. 1970), probably because of segregation and differential movement with respect to sex or spawning condition. The uneven sex ratio for 'ōmaka from Kāne'ohe Bay most likely results from movement into the bay of different fractions of each sex from a population that occurs in nearby offshore waters (or is in some other way not susceptible to capture by the nets used here). Most fish from overnight sets appeared to have been captured early in the morning, indicating that they had only recently moved into the bay. All the 'ōmaka captured, regardless of time of day, had empty or nearly empty stomachs, indicating that they had not been feeding for at least several hours before capture. This implies that they feed somewhere other than in the bay, and the reproductive condition of most females indicates that they were present in the bay primarily for spawning. Only spawning females were present during the day, but the night samples indicated that at least some of the previous day's spawners linger in the bay after spawning or are perhaps entrained with in-moving impending spawners. The day data indicated that spawning males outnumber females about 2 : 1, but this ratio could be even further biased if the spawning females were entering and leaving continually during the day but the males were present and susceptible to capture all day.

The potential biases in data on 'ōmaka from both day and night samples in the bay preclude an unequivocal estimate of spawning frequency of females. The day samples alone indicate that females spawn daily, but this clearly cannot be the case because there were both recent and impending spawners in the night samples. Furthermore, the night samples included a few females in neither group; this indicates that spawning frequency is less than 0.5/day, possibly much less if the putative population outside the bay includes a large fraction of such females. Clarke and Privitera (1995) estimated that spawning frequency was 0.33/day for *Selar crumenophthalmus*, a pelagic carangid similar to 'ōmaka in size and other aspects of reproductive biology.

Even though the uncertainty associated with estimated egg abundance on any given date was unknown, overall levels of egg abundance during the spawning season plus data on estimated fecundity allow estimates of the number and biomass of spawning females. Egg abundances during the peak periods of 1989 and 1990 were on the order of $1–2 \times 10^8$ and roughly twice that during 1991. Given the estimated fecundity, this means that about 135–270 kg or 870–1740 average-sized spawning females were present per day during the

first 2 yr, and 270–540 kg or 1740–3480 females per day in 1991. If, as suggested above, the population sex ratio is actually close to 1 : 1 and spawning frequency of female ʻōmaka is similar to that of *Selar crumenophthalmus* (0.33/day), the total population associated with the bay would be about six times higher, or about 800–1600 kg/5000–10,000 fish during 1989 and 1990 and about twice those values during 1991. These estimates are probably conservative because spawning frequency may be lower than 0.33/d, and it seems unlikely that individual fish, particularly females, spawn throughout the entire season or even the peak season. If, for example, individuals only spawned for 4–6 weeks, then the total population associated with the bay over an entire season would be several times larger than the above estimates.

Commercial catch data for ʻōmaka from Kāneʻohe Bay (provided by Hawaiʻi Division of Aquatic Resources) indicate that total reported annual catch was over 500 kg only twice since 1966 and was less than 250 kg for most years. The unreported commercial and recreational catch could well be comparable with the reported catch. A total catch of 500 kg would represent 30–60% of the estimated biomass for 1989 or 1990. Even if, as suggested by Watarai (1973) and Oakley and Bakhsh (1989*b*), ʻōmaka are rapid-growing fish and reach maturity at an age of about 18 months, the population appears to be heavily exploited, unless the biomass of fish associated with the bay over an entire season is considerably larger than the estimates above.

Although some ʻōmaka landed could be included with mixed, unidentified fish on catch reports, they do not appear to be seriously exploited in situations or times other than during the spawning season and in enclosed areas. Catch data from throughout Hawaiʻi indicate that ʻōmaka are reported almost exclusively from the same months they are present in Kāneʻohe Bay and from either Kāneʻohe Bay or similar enclosed habitats such as Pearl Harbor. Very few catches were reported during the winter months or from exposed coastal areas; the latter were all near likely spawning grounds.

Although several fishermen who have fished for ʻōmaka in the same way for over 30 yr in Kāneʻohe Bay agreed that catch per effort of ʻōmaka was much higher 20–30 yr ago, there is no independent evidence of a decrease in ʻōmaka abundance. Egg density estimates from surface plankton tows in the early 1970s (Watson and Leis 1974) are much lower than those encountered in this study, but this is almost certainly caused by ʻōmaka eggs being more abundant below the surface. The vertical egg samples from 1969 indicate egg densities comparable with those from this study and thus that abundance of adults has not changed substantially over the past 20 yr. Though the latter inference is somewhat tenuous and there is little reason to doubt the fishermen, it is possible that the decline in ʻōmaka catch and catch per effort was due to a change in behavior of the fish while in the bay. This is supported by initial efforts during this study to collect day samples by handline. These were unsuccessful even over areas where it was known from egg samples that hundreds of ʻōmaka were present, and it was necessary to resort to gill nets for day-caught fish. Kāneʻohe Bay has been subjected to several perturbations over the past 20–30 yr (e.g., Smith et al. [1981]); these may have in some indirect way resulted in a decrease in the residence time of spawning ʻōmaka or in the probability that ʻōmaka feed while in the bay.

ACKNOWLEDGMENTS

I am grateful to A. Alexander, R. Boland, M. Broom, K. Ching, R. Famble, and M. Minford for their assistance in many phases of the research and especially to L. Privitera for her analyses of reproductive biology.

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